Specialization of the motor system in infancy:

From broad tuning to selectively specialized purposeful actions

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RESEARCH HIGHLIGHTS

- We provide new insights into the developmental process of motor specialization, by which motor abilities, similarly to cognitive and perceptual functions, start out broadly tuned to their goal, becoming progressively more tailored to action goals over the first year of life.

- During purposeful action, 9-month-old infants activated multiple redundant limbs, whereas 12-month-olds were much more likely to restrict their goal-directed movements to a single arm.

- Increased specialization of limb movements was associated with greater selective attention and motor experience.

- Our findings indicate that extraneous movements accompanying purposeful actions have the potential to provide early motor markers of later neurocognitive deficits.

ABSTRACT

In executing purposeful actions, adults select sufficient and necessary limbs. But infants often move goal-irrelevant limbs, suggesting a developmental process of motor specialization. Two experiments with 9- and 12-month-olds revealed gradual decreases in extraneous movements in non-acting limbs during unimanual actions. In Experiment 1, 9-month-olds produced more extraneous movements in the non-acting hand/arm and feet/legs than 12-month-olds. In Experiment 2, analysis of the spatiotemporal dynamics of infants' movements revealed developmental declines in the spatiotemporal coupling of movements between acting and non-acting arms. We also showed that the degree of specialization in infants' unimanual actions is associated with individual differences in motor experience and visual attention, indicating the experience-dependent and broad functional nature of these developmental changes. Our study provides important new insights into motor development: as in cognitive domains, motor behaviours are initially broadly tuned to their goal, becoming progressively specialized during the first year of life.

Keywords: motor development, extraneous movements, motor overflow, specialization, infancy, reaching, action

Towards the end of the first year of life there are marked improvements in the ways in which infants use their limbs to act on the world across a range of behaviours, including manual exploration, reaching, intermanual coordination, and locomotion (e.g., Adolph & Berger, 2011; Fagard, 2000; Kimmerle, Ferre, Kotwica, & Michel, 2010; von Hofsten, 2007). Developmental theorists generally agree that such developments involve the increasing specificity and differentiation of the motor system during infancy (e.g., Gesell, 1954; Gibson & Pick, 2000; Sporns & Edelman, 1993; Thelen, 1985). The development of an ability to select efficient goal-directed movements has often been studied during reaching, focusing particularly on changes in the characteristics of movements within limbs (e.g., Bhat & Galloway, 2007; Konczak & Dichgans, 1997; Thelen et al., 1993; von Hofsten, 1991; for a review see Hadders-Algra, 2013). Yet, less attention has been paid to more broad-scale changes in action across the body, i.e., the transition from a less specialized state of motor selection in which multiple limbs are activated, to one in which only relevant limbs are selectively activated in the service of a goal (Soska, Galeon, & Adolph, 2012). In this report we focus on the development of limb selection during purposeful action; specifically, we examine for the progressive development of an ability to select only a single hand/arm during unimanual actions.

A growing body of evidence suggests that, early in development, the brain is "broadly tuned" to the environment (see Johnson, 2011, for an overview). In other words, it starts out functionally diffuse, with the response properties of neural regions being less selective to particular stimuli (i.e., less specialized). Thus, patterns of activation in the adult brain are more localised than those in the infant brain. Brain activation becomes increasingly specialized over developmental time through interactions between various brain regions and the environment (Edelman, 1987; Elman et al., 1996; Fair et al., 2007; Johnson, 2011; Supekar, Musen, & Menon, 2009). It is likely that motor development is yoked to brain

development and follows a similar trajectory, with motor ability being initially "broadly tuned" and becoming specialized over time. This gradual specialization likely happens in interaction with the environment through perception-action cycles (Gibson & Pick, 2000; Sporns & Edelman, 1993), leading to a better fit between action and environment.

Variable and overall movement abundance in early infancy is a hallmark of typical development, and the spontaneous movement repertoire of an infant provides insight into the early development of her/his nervous system (Einspieler & Prechtl, 2005). However, whereas spontaneous movements are typically assessed in the absence of interaction with an object, the goal of the current paper is to focus on how infants come to select particular limbs during purposeful actions towards an object. Previous work has shown that, in infants of 4.5-7.5 months of age (with no observed developmental changes in this period), actions with one hand are often accompanied by goal-irrelevant movements in other limbs, such as clenching, splaying, or wiggling of the fingers and toes (Soska et al., 2012). The production of these extraneous movements in the first months of life contrasts with the skilled purposeful movements of adults and even young children. However, developmental changes in extraneous movements in infancy remain undocumented and poorly understood. Thus we began our investigation with the hypothesis that the large prevalence of extraneous movements observed in young infants (Soska et al., 2012) may reflect a lack of specificity of the motor system, and that developmental decreases in such extraneous movements will signify the increasing specialization of the infant motor system. More specifically, we hypothesised that specialization (and thus reduction of extraneous movements) would occur particularly at the end of the first year of life, as part of the major developments in reaching, intermanual coordination, and locomotion seen at this time (e.g., Adolph & Berger, 2011; Fagard, 2000; Kimmerle et al., 2010; von Hofsten, 2007).

In Experiment 1, we began by measuring extraneous movements in non-acting limbs during unimanual reaching, predicting a developmental decrease in such movements between 9 and 12 months of age. Experiment 1 also investigated two factors which we expected to be related to the ability to select appropriate movements in infancy: individual differences in (i) motor experience, and (ii) selective attention. We were expecting decreases in extraneous movements to be specifically linked to the emergence of motor skills in which the use of the limbs is differentiated, such as walking with assistance. Therefore, we asked parents to report on their child's motor experience. We predicted that infants' motor experience would correlate negatively with extraneous movements in task irrelevant limbs.

The ability to visually select stimuli in the environment is known to be closely linked to motor processes in adult humans and non-human animals, with overlapping brain areas involved in attention shifts and movement preparation (Astafiev et al., 2003; Corbetta et al., 1998; Perry & Zeki, 2000; see also Allport, 1989; Rizzolatti & Camarda, 1987). Attention has also been implicated in the modulation of extraneous movements across the lifespan (for a review see Addamo, Farrow, Hoy, Bradshaw, & Georgiou-Karistianis, 2007). For example, children who are more easily distracted also produce more extraneous movements (Waber, Mann, & Merola, 1985). Furthermore, extraneous movements in adults increase when their attention is diverted (Baliz et al., 2005). A relationship between attention and extraneous movements has also been found in infants: looking more at an object during unimanual exploration was associated with fewer extraneous movements (Soska et al., 2012). To explore the relationship between attention and extraneous movements in more depth, we administered a well-established attention task (Gap-Overlap) to assess selection of visual information (Hood & Atkinson, 1993; Johnson, Posner, & Rothbart, 1991), predicting that greater difficulty with visual selection in the Gap-Overlap task would be associated with a higher prevalence of extraneous movements.

Experiment 1

We measured extraneous movements in non-acting limbs while infants were reaching with one hand (i.e., unimanually) for a ball. Measures of the proportion of unimanual reaches accompanied by extraneous movements were taken: (i) across the entire duration of the reach, and (ii) within +/- 100 ms of the onset of the unimanual reach to the ball, comparing groups of 9- and 12-month-old infants. Extraneous movements were also analysed in relation to infants' motor experience measured by parental report (how long infants had been sitting without support, crawling, standing with assistance, and walking with assistance), and infants' visual attention as measured by the Gap-Overlap task.

Methods

Participants

Two age groups, 9- and 12-month-olds, were tested in this experiment. The final sample size for Experiment 1 is presented in Table 1. Six additional infants were tested but excluded from analysis due to: (i) experimenter error (one 12-month-old), (ii) producing fewer than four unimanual reaches (three 9-month-olds, one 12-month-old), and (iii) not reaching for objects at all (one 9-month-old). The sample size in this study was consistent with sample sizes used in comparable studies (e.g., Adolph, 2000; Bhat & Galloway, 2007). The infants were recruited via a database of parents who expressed an interest in participating in developmental studies. Ethical approval was gained from the institutional research ethics committee. Prior to testing, informed consent was obtained from all parents. Testing only took place if the infant was awake and alert. The participants were given a small gift (e.g., a T-shirt) in return for their participation.

--Table 1 about here--

Procedure and materials

Reaching task. The infant was placed in an infant seat (Bébépod Flex, Prince Lionheart Inc., Santa Maria, CA, U.S.), and secured into place with adjustable straps around the waist so that movement of the trunk was restricted. There were 12 reaching trials in total. On each trial, the infant was presented with a 3.5 cm-diameter ball at the body midline, and at arm's length (calibrated for each infant) so that the infant could just grasp it without leaning forwards. The above measures were taken to prevent any potential compensatory movements in non-acting limbs resulting from changes in posture. The size of the ball was selected to induce unimanual reaching (see, e.g., Fagard, 2000). The ball's colour (white, orange, blue, green) was varied in a fixed random order between trials in order to maintain the infants' interest. Two video cameras operating at 100 Hz were used to record the infants' movements, each facing the infant either side of the midline. The movements were then coded offline.

For the purpose of the current study, only unimanual reaches were analysed. A coder selected unimanual reaches using the following discrimination criteria from Corbetta and Thelen (1996). Unimanual reaches had to comprise a unilateral extension of one arm (the acting arm) towards the target which was followed by contact with the target. To be counted as a unimanual reach, the other non-reaching arm was required to either remain still or produce non-target-oriented movements which remained at least a fist size away from the ball. On average, each 9-month-old contributed 8.3 unimanual reaches (*SD* = 2.7). Each 12-month-old contributed on average 9.8 unimanual reaches (*SD* = 2.1).

For each unimanual reach, the coder identified the timings of: (i) the onset of the reach (i.e., the moment when any part of the acting hand and/or arm from the fingertips to the shoulder started a continuous trajectory which ended in target contact), and (ii) contact (i.e., the moment when the hand touched the target for the first time in the trial). Next, the coder identified for each unimanual reach, whether any extraneous movement occurred. For the

purpose of Experiment 1, an extraneous movement in the hand/arm was any non-target oriented movement of the non-acting hand and/or arm (from the fingertips to the shoulder) which did not come within one fist size of the target ball. Most of these movements included one or more of the following: clenching, lifting, splaying, or wiggling of the fingers, twisting of the wrist, twisting or jerking of the arms. An extraneous movement in the feet/legs was any movement in a foot and/or leg (from the toes to the hips). Most of these movements included one or more of the following: clenching, lifting, splaying, or wiggling of the toes, flexion, extension, or rotation at the ankles, rotation at the knee, jerking of the leg (Soska et al., 2012). The feet/legs never touched the target or came within one fist's size of it. If there was an extraneous movement during the reach, then we coded whether it was tightly linked to the onset of movement in the acting limb (starting +/- 100 ms around the onset of the reach of the acting hand/arm). To compute inter-rater reliability, a second coder independently scored whether the reach was unimanual in 20% of all the reaches. Subsequently, the second coder scored for the presence of movement in the limbs not involved in the unimanual reach and whether they were tightly linked to the onset of the reach in 20% of the data. Inter-rater reliability was over 90%.

We calculated the proportion of unimanual reaches accompanied by extraneous movement for each infant. The measure was computed separately for the non-acting hand/arm and (the average across both) feet/legs. Furthermore, we calculated a proportion of reaches in which extraneous movement onset was tightly linked to the onset of movement in the acting limb (+/- 100 ms around the onset of the reach in the acting hand/arm). The proportion of unimanual reaches accompanied by these reach-onset-locked extraneous movements was computed separately for the non-acting hand/arm and (the average across both) feet/legs. Since these data were proportional, they were arcsine transformed prior to inferential analyses. Raw data are presented in the figures.

Gap-Overlap task. The infant was placed on his or her parent's lap approximately 65 cm from a 20" screen. The experimenter monitored and recorded the infant's looking behaviour from an adjacent room, via a video camera operating at 25 Hz. The eye movements were then manually coded offline. Before each trial, an attractive centrally-located stimulus (an "attention-getter") was displayed on the screen to attract the infant's attention. This was a square of black and white geometrical shapes changing in size (zooming in and out) accompanied by an interesting sound. Once the infant was looking at the attention-getter, the experimenter manually initiated a trial. On each trial, the attention-getter first disappeared and was replaced by a central fixation stimulus. After 800 ms, a peripheral target appeared on the left or right side of the screen and remained displayed for 1200 ms. In the Gap trials, the central fixation stimulus disappeared 200 ms prior to the onset of the peripheral target, thus leaving the screen blank for 200 ms before the appearance of the target. In the Overlap trials, the peripheral target appeared while the central fixation stimulus remained onscreen, leading to an overlap in time between these two stimuli. The central fixation and peripheral target stimuli were selected from a pool of four stimuli (pictures of balls visually matched on colour, attractiveness, and size [5.3 x 5.3 cm]). The pairs of pictures were presented to the infants in a pseudorandom order. Throughout the study, each stimulus was used an equal number of times as a central fixation and a peripheral target. The central fixation and the peripheral target were never the same stimuli within any given trial.

The Gap-Overlap task consisted of three blocks. In each block, eight Gap and eight Overlap trials were presented, thus 16 trials in each block, and 48 trials in total. The order of presentation of the Gap and Overlap trials was randomized within each block. Trials were considered invalid if: (i) the infant did not look at the central stimulus immediately before the presentation of the peripheral target; and/or (ii) the infant did not look at the peripheral target within the duration of the trial. Inter-rater reliability calculated over 20% of the data was 98%

for the validity of trials and 92% for saccadic reaction times. We decided *a priori* to exclude reaction times under 150 ms or over 1200 ms (e.g., see Csibra, Tucker, & Johnson, 1998; Wass, Porayska-Pomsta, & Johnson, 2011).

Nine-month-olds contributed an average of 14.2 valid Gap trials (*SD* = 4.7) and 13.4 valid Overlap trials (*SD* = 4.7). Twelve-month-olds contributed on average 15 valid Gap trials (*SD* = 4.9) and 14.1 valid Overlap trials (*SD* = 4.4). The "Gap effect" (the difference in reaction times between Gap and Overlap trials) was computed for each infant as a measure of efficiency of disengaging from a central visual stimulus to orient to a peripheral one. Outliers below and above 2 *SD* were excluded from the data set. The Gap effect was 86 ms (*SD* = 39 ms) for 9-month-olds and 81 ms (*SD* = 30 ms) for 12-month-olds.

Motor experience scoring. The amount of experience with motor skills was reported by parents in a custom interview (reporting on sitting without support, crawling, standing with assistance, walking with assistance, standing alone, walking alone; Wijnhoven et al., 2004). The parents were encouraged to use baby books, calendars, pictures, and videos to facilitate their memories (Adolph, 2002). An experimenter also confirmed that the infants could perform the motor skills listed above. A motor experience score was computed based on experience with a range of skills which were present in more than half of the infants tested in each age group. The resultant skills which were included in this measure were: sitting without support, crawling, standing with assistance, walking with assistance. The number of months' experience with each of these skills was summed for each infant to yield a "motor experience score". Outliers below and above 2 *SD* were excluded from the data set. On average, the motor experience score was 7.1 (*SD* = 4.5) for 9-month-olds and 12.1 (*SD* = 4.6) for 12-month-olds.

Results

Reaching task

Throughout the reach, we identified significantly more extraneous movements in the non-acting hand/arm in 9-month-olds compared to 12-month-olds, $t(36) = 3.27$, $p = .002$, $d = 1.09$ (Figure 1a). Nine-month-olds also moved their feet/legs during a greater proportion of unimanual reaches than 12-month-olds, $t(36) = 2.78$, $p = .009$, $d = 0.93$ (Figure 1b).

--Figure 1 about here--

Traces of motor activity in extraneous limbs which are closely linked to the onset of purposeful movement have been observed in children and adults (Koerte et al., 2010; for a review see Addamo et al., 2007). Such movements have been characterized as reflecting a motor command which overflows from one limb to others (Addamo et al., 2007). This "motor overflow" in children and adults is typically observed during difficult motor tasks, and very much smaller in amplitude than the extraneous movements in infants documented here and elsewhere (Soska et al., 2012). In order to investigate the presence of motor overflow, we examined the extent to which the onsets of infants' extraneous movements were tightly linked to reach onsets by reporting extraneous movements with an onset within a window of +/- 100 ms around reach onset (henceforth, "tightly linked extraneous movements"). Within this window, 9-month-olds continued to show a higher proportion of unimanual reaches accompanied by the onset of extraneous movements in the non-acting hand/arm than 12-month-olds, $t(36) = 5.36$, $p < .001$, $d = 1.79$ (Figure 1a). A trend in the same direction was also observed with tightly linked extraneous movements in feet/legs, $t(36) = 1.81$, $p = .078$, $d = 0.61$ (Figure 1b).

Extraneous movements, selective attention, and motor experience

A multiple regression analysis was conducted to evaluate whether age, selective attention, and/or motor experience predicted extraneous movements in the non-acting

hand/arm. Using the Enter method, it was found that the linear combination of all three predictors explained a significant amount of the variance in both overall and tightly linked extraneous movements in the non-acting hand/arm (overall: R^2 = .52, F(3, 29) = 10.33, p < .001; tightly linked: R^2 = .61, F(3, 28) = 14.60, p < .001). Age and selective attention made a significant contribution to the prediction equation, while motor experience did not, for overall extraneous movements in the non-acting hand/arm (age: t(29) = -3.81, p < .001; selective attention: t(29) = 3.48, p = .002; motor experience: t(29) = 0.72, p = .479), and also for tightly linked extraneous movements in the non-acting hand/arm (age: t(28) = -5.21, p < .001; selective attention: t(28) = 2.98, p = .006; motor experience: t(28) = 1.09, p = .283). To confirm that selective attention explained a unique proportion of variance, we conducted a hierarchical regression that initially only included age as a predictor. The addition of selective attention as a predictor led to a significant increase in the proportion of variance explained (overall: change in R^2 = .24, F(1,30) = 14.47, p < .001, Table 2a; tightly linked: change in R^2 = .16, F(1,29) = 11.14, p = .002, Table 2b). Thus, the greater the Gap effect (i.e., the more difficulty infants had with visual selection), the more extraneous movements (overall, as well as tightly linked to movement onset) they produced in their non-acting hand/arm.

--Table 2 about here--

A multiple regression analysis was conducted to evaluate whether age, selective attention, and/or motor experience predicted extraneous movements in feet/legs. Using the Enter method, it was found that the linear combination of all three predictors explained a significant amount of the variance in overall extraneous movements in the feet/legs, but this time not in extraneous movements which were tightly linked to movement onset (overall: R^2 = .40, F(3, 29) = 6.47, p = .002; tightly linked: R^2 = .18, F(3, 29) = 2.14, p = .117). For overall

extraneous movements in feet/legs, only motor experience made a significant contribution to the prediction equation, while age and selective attention did not (motor experience: $t(29) = -3.00$, $p = .005$; age: $t(29) = -1.31$, $p = .202$; selective attention: $t(29) = 1.36$, $p = .185$; see Table 3). Thus, the more experience infants have with motor skills, the fewer overall extraneous movements in feet/legs they produced.

--Table 3 about here--

To disentangle which type of motor experience (out of: sitting without support, crawling, standing with assistance, and walking with assistance) predicts overall extraneous movements in feet/legs, we carried out additional multiple regression analyses. Using the Enter method, it was found that the linear combination of all four predictors explained a significant amount of the variance in overall extraneous movements in feet/legs, $R^2 = .50$, $F(4, 26) = 6.57$, $p < .001$. Crawling and walking with assistance made a significant contribution to the prediction equation, while sitting without support and standing with assistance did not (crawling: $t(26) = -2.24$, $p = .034$; walking with assistance: $t(26) = -2.15$, $p = .041$; sitting without support: $t(26) = -0.10$, $p = .923$; standing with assistance: $t(26) = 1.77$, $p = .089$; see Table 4a). This therefore suggests that locomotor experience is predictive of the decrease of extraneous movements in feet/legs but not, as shown earlier, in the hands/arms. A stepwise regression revealed that crawling and walking with assistance do not contribute a unique proportion of variance, with crawling being a significant predictor in this entry method, $R^2 = .42$, $F(1, 31) = 22.62$, $p < .001$, $t(31) = -4.76$, $p < .001$, see Table 4b.

--Table 4 about here--

Experiment 2

Experiment 1 revealed a developmental decrease in extraneous movements during reaching between 9 and 12 months of age. We also observed that a large proportion of 9-month-olds' unimanual reaches were accompanied, at their onset (+/- 100 ms), by extraneous movements in the non-acting hand/arm. These onset-locked movements are likely the developmental precursor of the motor overflow seen in older children and adults during demanding actions (Addamo et al., 2007).

In adults, when a unilateral motor command is generated in one hemisphere, the interhemispheric connections of the corpus callosum usually inhibit the corresponding area in the other hemisphere (Grefkes, Eickhoff, Nowak, Dafotakis, & Fink, 2008). Thus, it has been argued that symmetrical control of the two hands is surmounted via inhibitory processes (Dennis, 1976; Duque et al., 2007). However, inhibitory processes are limited in infancy and some have suggested (e.g., Fagard, 1998; Goldfield & Michel, 1986; Goldfield & Wolff, 2004) that symmetrical activation of the hands is a general principle of action in early infancy. Therefore, we should also witness more symmetrical spatiotemporal congruency between acting and non-acting arms in young infants compared to older infants. Experiment 2 tested this hypothesis by examining the spatiotemporal congruency between the acting and non-acting arms. Using motion capture, we measured in fine detail the spatiotemporal coupling between movements in acting and non-acting hands/arms during the action of shaking a rattle with a single hand in 9- and 12-month-olds. We predicted the presence of spatiotemporal coupling (symmetrical about the body midline) in 9-month-olds, which would be significantly reduced in 12-month-olds. A key advantage of the rattling action is that it allows greater confidence that any extraneous movements are an unintended outcome of the action. Many studies of reaching behaviour (Experiment 1 included) have to make assumptions about

whether infants intended the reach towards objects to be with one or two hands (see Fagard & Pezé, 1997). With unimanual rattle shaking, intention to act bimanually is extremely unlikely.

In adults, the interhemispheric inhibition responsible for suppressing bilateral motor activation is down-regulated as the effort required for a motor response increases (Perez & Cohen, 2008; Tinazzi & Zanette, 1998). Thus, we also investigated in the infants the effect of effort (speed of shaking) (Bodwell, Mahurin, Waddle, Price, & Cramer, 2003; Morrison, Hong, & Newell, 2011) on spatiotemporal congruency during rattle shaking. If increased speed of shaking is related to increases in between-arm congruency in infants, this would suggest that the developmental suppression of extraneous movements in infancy is driven at least in part by inhibitory processes.

Methods

Participants

The 9- and 12-month-olds recruited for Experiment 1 were also asked to participate in Experiment 2. The sample size for Experiment 2 is presented in Table 1. In Experiment 2, ten infants (in addition to those reported in Table 1) were tested but excluded from analysis because: (i) they produced fewer than four shaking sequences (six 9-month-olds, two 12-month-olds) and (ii) due to equipment failure (one 9-month-old, one 12-month-old). The sample size in this study was consistent with sample sizes used in comparable studies (e.g., Adolph, 2000; Bhat & Galloway, 2007).

Procedure and materials

In Experiment 2, the infant was placed in the same infant seat as used in Experiment 1, and secured with adjustable straps around the waist so that movement of the trunk was restricted. The rattle (which was 19 cm in length, and 6.7 cm in diameter at its widest point) was presented to the infant. Following extensive piloting with several types of rattle, this particular rattle was selected as being the one which produced the greatest amount of

unimanual shaking in the infants. We alternated between giving the infants each of two different versions (one was opaque, the other transparent, but they were otherwise identical) of the same rattle in order to maintain their engagement in the task. At the beginning of each trial, the experimenter demonstrated the shaking of a rattle and placed the rattle in the infant's left or right hand to facilitate unimanual shaking. The side of presentation was presented in a novel pseudorandom order for each participant (with the constraint that the rattle could not be placed in the same hand more than twice consecutively). There were 6 shaking trials in total, each lasting 30 seconds.

Movement of the arms during shaking was recorded using an eight-camera OptiTrack motion capture system operating at 100 Hz (NaturalPoint, Inc., Corvallis, OR, U.S.). Six of the cameras recorded position–time data from both arms while two cameras served as video cameras (100 Hz). This allowed us to obtain motion capture data synchronized with video footage. Cameras were placed surrounding the infant. The reference frame of the system was set relative to the infant, such that the *x*-axis (horizontal) corresponded to the left-right axis of the body (left shoulder to right shoulder). We observed very little trunk rotation, which might otherwise have misaligned the body left-right axis with the reference *x*-axis. Likewise, the *y*-axis (vertical) corresponded to the vertical axis of the body, and we observed very little forward trunk sway which might otherwise have misaligned the body and room vertical axes.

To capture the position of the arms, two custom-made rigid bodies were constructed. Each was made up of an array of four reflective markers (each 15.88 mm in diameter) placed in fixed positions on a small non-reflective plastic board (550 x 550 mm). The rigid bodies were each mounted on a velcro strap which was used to secure them to the infants' forearms (one on each arm).

From the video records, the coder selected unimanual shaking sequences which were at least 2 seconds long, when one hand was shaking the rattle on one side of body while the

other hand was not touching the rattle and free to move on the other side of the body. The motion capture data were analysed offline. At each frame the 3D positions of the centre of each of the rigid bodies were calculated using the system's analysis software ("Tracking Tools", NaturalPoint Inc., Corvallis, OR, U.S.). Further analyses were performed with customized Matlab routines (Mathworks Inc., Natick, MA, U.S.). For each shaking sequence, the position of the centre of the rigid body on *x*-, *y*-, and *z*-axis was plotted and then visually inspected to identify shaking sequences which did not contain sufficient data for further analysis (e.g., due to occlusion of motion capture markers). Segments of data with significant artefacts (e.g., spikes) were detected visually and deleted. Next, the data were interpolated using a cubic spline function and filtered using a second-order low pass Butterworth filter operating at 8 Hz.

As a measure of spatiotemporal congruency between the arms, we calculated the correlation at each time point between the positions of the acting and non-acting arms on the horizontal (*x*) and vertical (*y*) axes for every shaking sequence (following Fagard & Pezé, 1997). We focused on the *x*- and *y*-axes, because shaking did not typically involve significant movement in depth (the *z*-axis). On the vertical (*y*) axis, a higher positive correlation indicates greater spatiotemporal congruency (e.g., as one arm moves up, the other also moves up, see Figure 2a). On the horizontal (*x*) axis, negative correlations indicate greater spatiotemporal symmetry about the body midline (e.g., as one arm moves right, the other moves left, see Figure 2b). Outliers above and below 2 *SD* were excluded from the data set. Because the data were bounded between -1 and 1, they were arcsine transformed. The raw data are presented in the figures.

The average speed of the shaking arm was computed for each shaking sequence. In order to examine the role of shaking speed in spatiotemporal coupling between acting and non-acting arm movements, a median split (*Mdn* = 287 mm/sec) was performed on speed of

the shaking arm to divide shaking sequences into a slower half (M = 187 mm/sec, SD = 64 mm/sec; henceforth "slow") and a faster half (M = 431 mm/sec, SD = 120 mm/sec; henceforth "fast").

Correlations in the vertical and horizontal axes for every sequence were used in the statistical analyses. In total, 242 unimanual shaking sequences were available for the analyses (9-month-olds: 126 shaking sequences; 12-month-olds: 116 shaking sequences). On average, each 9-month-old contributed 9 shaking sequences (SD = 5.9). Each 12-month-old contributed on average 6.1 shaking sequences (SD = 4.9).

Results

Vertical axis

The shaking sequences were entered into a 2 x 2 analysis of variance (ANOVA) examining the effect of Age (9- versus 12-month-olds) and Speed (of the acting arm; slow versus fast) on correlation scores in the vertical axis. The ANOVA revealed a main effect of Age, indicating more positive correlation scores in the shaking sequences of 9-month-olds than those of 12-month-olds, $F(1, 238) = 6.90$, $p = .009$, $\eta_p^2 = .03$. Furthermore, there was a main effect of Speed indicating that correlation scores were more positive with speed, $F(1, 238) = 20.51$, $p < .001$, $\eta_p^2 = .08$. There was also an interaction between Age and Speed, $F(1, 238) = 8.07$, $p = .005$, $\eta_p^2 = .03$. At a slow speed, 9-month-old's shaking sequences showed more positive correlation scores than those of the 12-month-olds, $t(119) = 3.57$, $p = .002$, $d = 0.66$ (p-value Bonferroni corrected) (see Figure 2c). But there was no significant difference between Ages for fast speed. While 9-month-olds did not show a difference in correlation scores between slow and fast speed movements, correlation scores at 12 months were significantly more positive for fast speed compared to slow speed movements, $t(114) = 4.56$, $p < .001$, $d = 0.87$ (p-value Bonferroni corrected) (see Figure 2c).

One-sample *t*-tests of correlation scores against zero (i.e., no correlation; see Figure 2c) revealed that correlation scores were significantly more positive than zero for both slow and fast speeds in 9-month-olds, $t(51) = 3.17$, $p = .012$, $d = 0.44$; $t(73) = 6.52$, $p < .001$, $d = 0.76$ (*p*-values Bonferroni corrected). This was also true for 12-month-olds, but only for fast speed movements, $t(46) = 4.58$, $p < .001$, $d = 0.67$ (*p*-value Bonferroni corrected).

Horizontal axis

The shaking sequences were entered into a 2 x 2 ANOVA examining the effect of Age (9- versus 12-month-olds) and Speed (of the acting arm; slow versus fast) on correlation scores in the horizontal axis. The ANOVA revealed a main effect of Age, indicating more negative correlation scores in the shaking sequences of 9-month-olds than those of 12-month-olds, $F(1, 238) = 9.01$, $p = .003$, $\eta_p^2 = .04$. There was no main effect of speed or interaction between Age and Speed.

One-sample *t*-tests of correlation scores against zero (i.e., no correlation; see Figure 2d) revealed that correlation scores were significantly negative with respect to zero for fast speed movements in 9-month-olds, $t(73) = -2.72$, $p = .032$, $d = 0.32$ (*p*-value Bonferroni corrected). But slow movements in 9-month-olds and both slow and fast movements in 12-month-olds were not significantly different from zero.

--Figure 2 about here--

General discussion

We have documented for the first time a substantial decrease in extraneous movements accompanying unimanual object-directed reaching between 9- to 12-months of age (Experiment 1). This developmental trend is reflected in a simultaneous decrease in the spatiotemporal congruency of movements between the arms during unimanual shaking

(Experiment 2). We argue that both findings reflect a wider developmental process of gradual motor specialization over the first year of life, in which infants' motor responses to action goals become increasingly tailored to their purpose, resembling the developmental processes of specialization seen in other domains including language and face processing (Gervain & Mehler, 2010; Lewkowicz & Ghazanfar, 2009; Maurer & Werker, 2014; Pascalis et al., 2005; Scott & Monesson, 2010; Werker & Tees, 1984; for a review see Johnson, 2011). The "broad tuning" of the motor system early in development is likely shaped through interactions with the environment (Gibson & Pick, 2000; Sporns & Edelman, 1993). For example, in Experiment 1, 9-month-olds activated multiple limbs even though only one of the hands successfully retrieved the object. It is likely that feedback about which limb was successful at retrieval over many repetitions gives rise to the ability to retrieve an object unimanually without activating any other limb. This would lead to a decrease in extraneous movements by 12 months of age. However, the current paper focused specifically on arm movements in reaching and shaking. Future research should explore the emergence of specialization in different motor sub-domains, which may differ in developmental timing.

What developmental processes underlie this motor specialization? The increases in inter-limb congruency with speed observed in Experiment 2 point to a role for inhibition in the modulation of extraneous movements (Addamo et al., 2007; Hoy, Fitzgerald, Bradshaw, Armatas, & Georgiou-Karistianis, 2004; Perez & Cohen, 2008). It may be that brain changes underlying the development of inhibitory connections between two hemispheres can explain the changes in extraneous movements observed in Experiments 1 and 2. The main brain structure responsible for interhemispheric inhibition is the corpus callosum, and this develops across early life reaching its adult size and myelination in later adolescence when extraneous movements typically decline to an adult level (for a review see Addamo et al., 2007; Giedd et al., 1999). It has also been implicated in the development of a range of motor behaviours such

as laterality (e.g., Sacco, Moutard, & Fagard, 2006). Moreover, the development of the corpus callosum and developmental decreases in extraneous movements might both be related to the development of intermanual coordination abilities (Muetzel et al., 2008). However, it is very likely that other neurodevelopmental changes (e.g., pruning in ipsilateral corticospinal projections; Eyre, Taylor, Villagra, Smith, & Miller, 2001; Martin, 2005) contribute to explaining the wider range of changes in motor specialization.

In adults, the brain areas involved in movement preparation overlap substantially with those implicated in selective attention (Astafiev et al., 2003; Corbetta et al., 1998; Perry & Zeki, 2000; see also Allport, 1989; Rizzolatti & Camarda, 1987). Here, we found that infants with a greater ability to disengage from a familiar visual stimulus and shift attention to a new event were better able to produce movements more specifically tailored to their action goals (i.e., fewer extraneous movements), indicating an overlap in early life between processes of selective attention and movement (e.g., Bacher & Robertson, 2001; Robertson & Johnson, 2009). The emerging ability to shift attention between sensory stimuli which occurs during the first months of life (Colombo, 2001; Richards & Casey, 1992) likely provides the crucial foundation for the selective processes required in the motor skills, which continue to be perfected well beyond infancy (Addamo et al., 2007; Koerte et al., 2010).

Finally, our finding of a link between greater motor experience and fewer extraneous movements in the feet/legs suggests that motor specialization (as with specialization in other domains; Johnson, 2011) is an experience-dependent process. It is interesting to note that the locomotor skills were the most related to a reduction in extraneous movements in feet/legs. Given that the acquisition of locomotor skills places a particular burden on learning to move the feet/legs independently, the particular coupling between motor skills and extraneous movements of the feet/legs reinforces the view that motor learning is specific to the mode of action (Adolph, 2000). Further research will be needed to determine how motor experience

interacts with the neural mechanisms described above and which, we suggest, underlie the development of motor specialization. A better understanding of the developmental processes underlying motor specialization has great clinical significance since aggravated extraneous movements have been described in various clinical populations including children with attention-deficit/hyperactivity disorder (e.g., D'Agati, Casarelli, Pitzianti, & Pasini, 2010; MacNeil et al., 2011) and autism (e.g., Jansiewicz et al., 2006).

Why do infants produce extraneous movements during purposeful action? In fact we consider it highly likely that, far from being extraneous, such movements serve adaptive purposes in early life. It may be that such movements are a vestige of our evolutionary past. Movements in the feet/legs during reaching and manipulation (Soska et al., 2012) could be driven by a phylogenetically older, quadrupedal system of movement (see Dietz, 2002). It is possible that the dramatic decline in such extraneous feet/legs movements observed here may signify the progression to a more recently evolved mode in which the manual system operates independently of quadrupedal movement (Dietz, 2002). Similarly, but without the proposal of an independent manual system, it may be that infants become gradually more competent at controlling redundant degrees of freedom and developing efficient movement synergies (see Bernstein, 1967; Sporns & Edelman, 1993). Irrespective of this question, however, it is likely that extraneous movements play an adaptive role in ontogenetic development. It may be that the broad motor tuning reflected by extraneous movements facilitates specialization by enabling the selection of the most efficient movements for a given action as sensorimotor experience progresses. A further possibility is that extraneous movements provide motor activity and reafferent sensory feedback which is crucial to activity dependent processes of development in the nervous system (see Blumberg, 2015).

The current paper provides important new insights into the processes whereby infants become able to select appropriate limb movements in the service of purposeful action. In the

early stages of learning to act on the world, the infant motor system appears to be “broadly tuned”, but over the first year of life, motor responses become progressively more specialized. We argue that this broad motor tuning in early infancy likely fulfils an adaptive function by providing young infants with a wide repertoire of responses to their environment from which they can select the most effective over the coming months of life. The process of motor specialization documented here has wide-reaching implications for the development of a range of motor abilities such as object exploration, locomotion, intermanual coordination, the emergence of lateralised action, and tool use.

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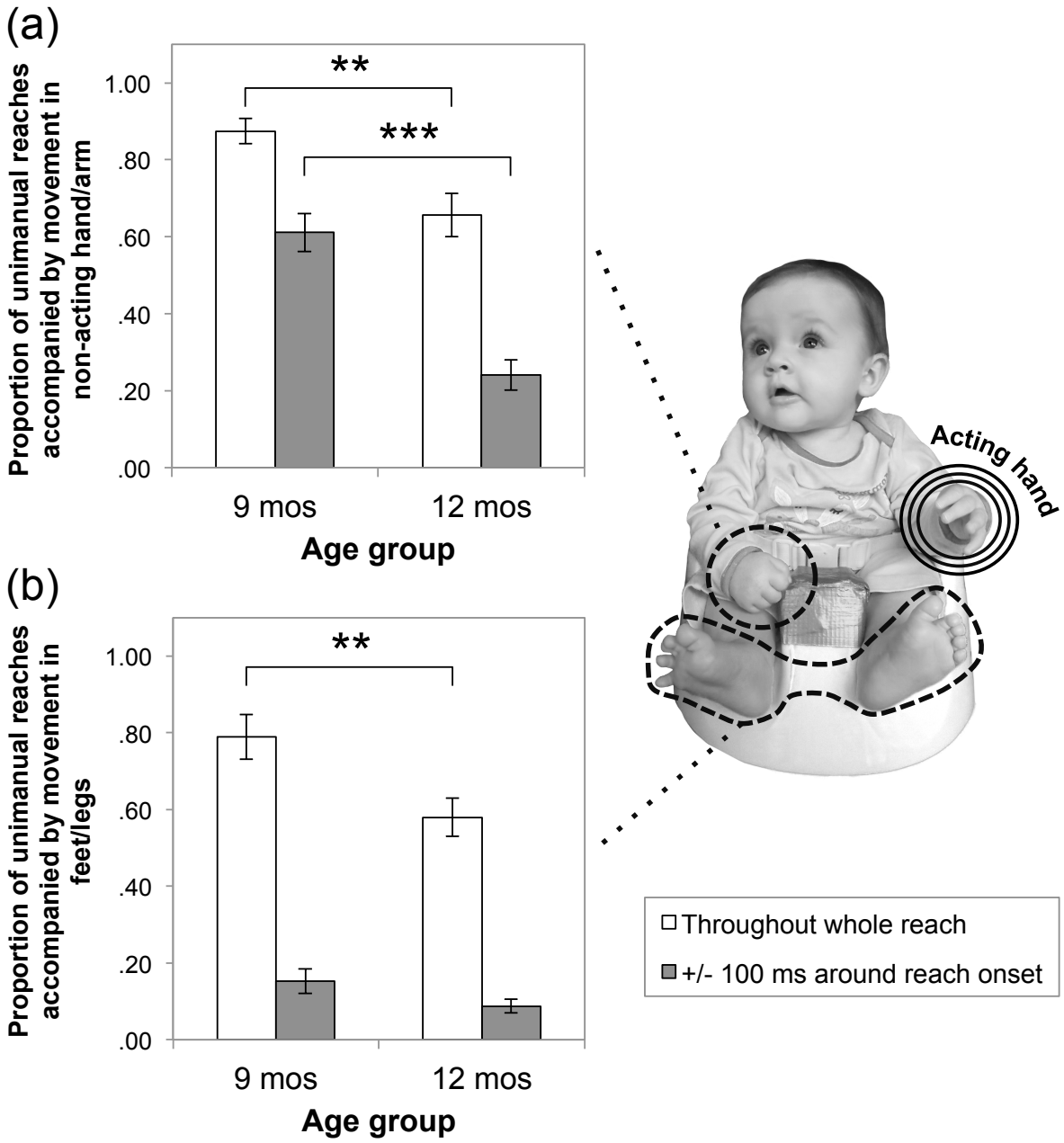

Figure 1: Experiment 1. Proportion of unimanual reaches accompanied by movements in non-reaching limbs, for 9- and 12-month-olds. (a) Overall movements observed in the non-acting hand/arm throughout the reach, and movements in the non-acting hand/arm with an onset that is tightly linked to the onset of the reach (+/- 100 ms). (b) Overall movements in the feet/legs throughout the reach, and movements in the feet/legs with an onset that is tightly linked to the onset of the reach (+/- 100 ms). Error bars show +/- 1 *SE*; **p* < .05, ***p* < .01, ****p* < .001.

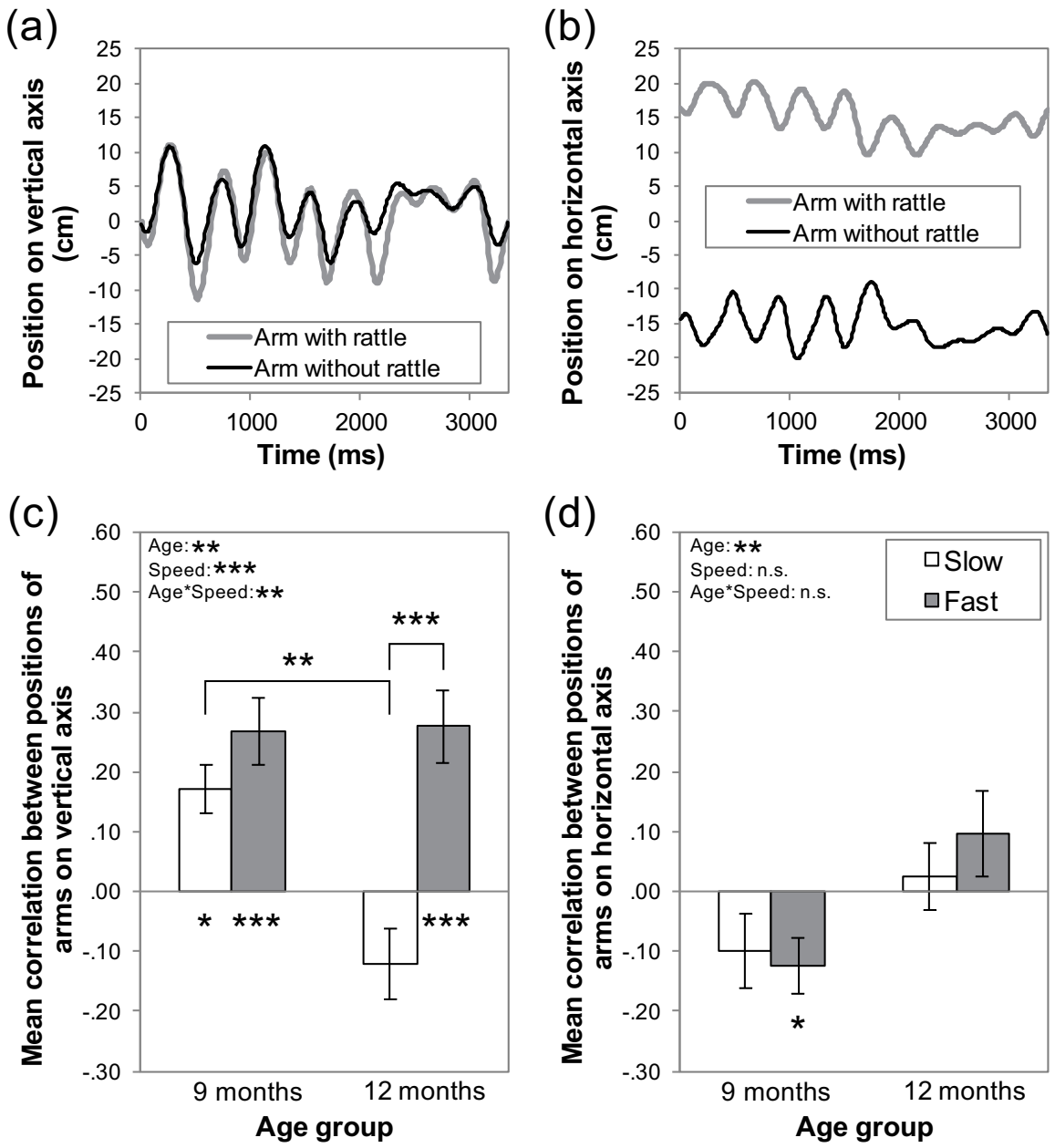

Figure 2: Experiment 2. Correlation scores for unimanual rattle-shaking movements. (a) An example of a rattle-shaking sequence where acting and non-acting arms show large positive correlation on the vertical (*y*) axis indicating that they were moving up and down in synchrony (the correlation between positions of the arms is .92). (b) An example of a rattle-shaking sequence where acting and non-acting arms show moderate negative correlation on the horizontal (*x*) axis indicating that they were moving in symmetry about the midline (the correlation between positions of the arms is -.39). (c) Correlation scores on the vertical axis during shaking in 9- and 12-month-olds for slow speed and fast speed of shaking. (d) Correlation scores on the horizontal axis during shaking in 9- and 12-month-olds for slow speed and fast speed of shaking. Error bars show +/- 1 *SE*; $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$.

Table 1: Participant characteristics in Experiments 1 and 2

	Age group	n	Sex	Mean age (months)
Experiment 1	9-month-olds	18	9f, 9m	8.88 (*SD* = 0.30)
	12-month-olds	20	8f, 12m	12.14 (*SD* = 0.32)
Experiment 2	9-month-olds	14	8f, 6m	8.90 (*SD* = 0.31)
	12-month-olds	19	7f, 12m	12.19 (*SD* = 0.28)

Table 2: Hierarchical regression analysis (Enter method) for variables predicting (a) overall movements observed in the non-acting hand/arm during the reach, and (b) movements in the non-acting hand/arm with an onset that is tightly linked to the onset of the reach (+/- 100 ms).

(a)

	B	*SE B*	β
Model 1			
Constant	2.419	0.433	
Age	-0.138	0.041	-.520**
Model 2			
Constant	1.869	0.390	
Age	-0.136	0.034	-.511***
Selective attention	0.006	0.002	.487***

Note: R^2 = .27 for Model 1 (p < .01); ΔR^2 = .24 for Model 2 (p < .001).
**p < .01, ***p < .001.

(b)

	B	*SE B*	β
Model 1			
Constant	1.727	0.272	
Age	-0.123	0.025	-.661***
Model 2			
Constant	1.431	0.251	
Age	-0.122	0.022	-.658***
Selective attention	0.003	0.001	.395**

Note: R^2 = .44 for Model 1 (p < .001); ΔR^2 = .16 for Model 2 (p < .01).
**p < .01, ***p < .001.

Table 3: Multiple regression analysis (Enter method) for variables predicting overall movements in the feet/legs during the reach.

	B	*SE B*	β
Constant	1.697	0.473	
Age	-0.059	0.046	-.214
Selective attention	0.003	0.002	.201
Motor experience	-0.045	0.015	-.504**

Note: R^2 = .40 (p < .01). **p < .01.

Table 4: Multiple regression analysis for motor experience variables predicting overall movements in the feet/legs during the reach: (a) Enter method and (b) Stepwise method.

(a)

	B	*SE B*	β
Constant	1.060	0.182	
Sitting without support	-0.004	0.042	-.019
Crawling	-0.099	0.044	-.439*
Standing with assistance	0.069	0.039	.275
Walking with assistance	-0.182	0.084	-.378*

Note: R^2 = .50 (p < .001). *p < .05.

(b)

	B	*SE B*	β
Constant	1.215	0.099	
Crawling	-0.149	0.031	-.650***

Note: R^2 = .42 (p < .001). ***p < .001.